

A REVISION OF PETALONYX (LOASACEAE) WITH
A CONSIDERATION OF AFFINITIES IN
SUBFAMILY GRONOVIOIDEAE

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Petalonyx is a genus of shrubs and sub-shrubs of the desert and semi-arid regions of the southwestern United States and Northern Mexico. Although a few modern floras give good accounts of some of the species, no monograph treating the entire genus has been prepared. Apparently *Petalonyx* has not invited the attention of monographers because the species are relatively distinct and hence new collections are not difficult to identify. Nevertheless, it is remarkable that taxonomists have been content merely to describe the flowers of *Petalonyx* as having the stamens located outside the corolla tube without attempting to understand such unorthodox morphology. Our attention was first drawn to *Petalonyx* during the general survey of the family to determine generic limits preparatory to a more detailed study of *Mentzelia*. Although we encountered no difficulty in delimiting *Mentzelia* from *Petalonyx* we did raise some questions concerning the generic affinities of *Petalonyx* with the other members of subfam. Gronovioideae. In addition to the five species of *Petalonyx*, subfam. Gronovioideae accommodates the one species of *Cevallia*, the two species of *Gronovia*, and the one species of *Fuertesia* (Urban and Gilg, 1900). Although our interest has been centered on *Petalonyx* we have extended our observations to the other genera of this subfamily whenever possible.

Four of the five species of *Petalonyx* have been studied as living plants in natural populations and only *P. crenatus* of north central Mexico remains unknown to us as living material. *Cevallia* has been studied in two natural populations and one species of *Gronovia* has been grown in our greenhouse. Thus we have had living material of six of the nine species of subfam. Gronovioideae, making cytological and anatomical studies possible. Chromosomes were examined by fixing anthers in 3:1 ethanol-acetic acid, squashing in acetocarmine, and observing with a phase microscope. Anatomical studies were made from material either embedded in paraffin and sectioned or simply cleared in lactic acid. Voucher specimens for our chromosome number determinations are on file in the herbarium of the University of California, Los Angeles (LA). We have examined all the specimens of *Petalonyx* from the following herbaria: BAYLU, DAS, DS, GH, LA, LL, POM, RSA, SMU, TAES, TEX, US. The manuscript benefited greatly from the critical comments of Peter H. Raven and Wallace R. Ernst. This study was supported by Grant GB-1337 from the National Science Foundation.

PETALONYX

Some of the features of *Petalonyx* are of particular interest and will be singled out here for detailed consideration while a later section of this paper will present a formal taxonomic treatment with descriptions and keys. The flowers of the five species are borne in naked or bracted racemes and are generally similar in their inferior, unilocular ovary with a single, pendulous ovule. No matrix tissue proliferates in the lumen between the developing seed and the ovary wall and there is no disc at the apex of the ovary. The fruit is indehiscent and the mature seed is pyriform, lacks endosperm, and has a smooth to finely striated testa. The cotyledons are ovate and the inner surfaces are smooth. The simple style and stigma and the calyx, which is deeply divided into five lanceolate lobes, also are quite uniform throughout the genus. In contrast, the petals and stamens exhibit some unusual features that distinguish some of the species. *Petalonyx nitidus*, *P. thurberi*, and *P. parryi* are distinctive by their apparently sympetalous corollas with the anthers outside the corolla tube (fig. 1). *Petalonyx crenatus* is unique in having only two functional stamens and the flower is thus bilaterally symmetrical (fig. 1). *Petalonyx linearis* remains distinct by its orthodoxy for it lacks these unusual characters. Certain morphological features, whose modifications provide these unusual floral differences, are present throughout the genus. The petals in all species are clawed and each side of the claw has two narrow flaps of tissue, one inner and one outer, that extend laterally toward the adjacent petals (fig. 2e). The stamens are not in themselves unusual, being composed of a slender filament with a terminal, 4-chambered anther, however the filaments arise from the short hypanthium opposite the sepals and between, but apparently in the same whorl with, the petals (fig. 2a). In bud the low portions of the filaments are held between the inner and outer flaps of adjacent petal claws (fig. 2b-f) while the distal portion of the filaments and the anthers are enclosed by the petal limbs (fig. 2g). In *P. thurberi*, *P. nitidus*, and *P. parryi* the inner flaps of tissue of adjacent petals remain free near the base (fig. 2b) but become firmly connivent along the upper half of the claw thus forming a corolla tube (fig. 2c-e). As the buds open, the staminal filaments are freed to incline outward while the petals remain held together—hence the unusual condition of the stamens outside the corolla tube. Although the claws become strongly connivent and sometimes can be pulled apart only by tearing tissue, it is clear that they are secondarily adhered together because the cuticle that covers the epidermis is continuous through the point of connection of adjacent claws. Although the petal claws in *P. linearis* and *P. crenatus* have the flaps of tissue, they do not become connivent in these species, no tube is formed, and the stamens are not held outside of the corolla.

The cross sections of the flowers also revealed a difference in the vascularization of the style. In *P. thurberi*, *P. nitidus*, and *P. parryi*

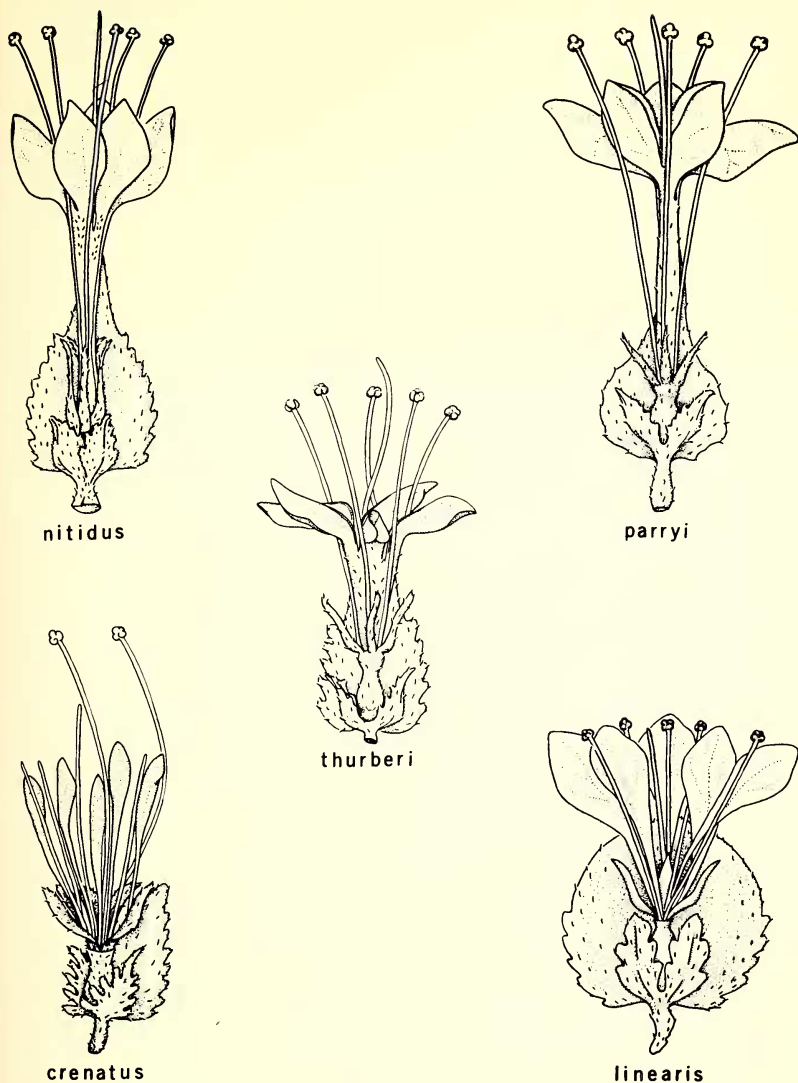


FIG. 1. Drawings of flowers and bractlets of the five species of *Petalonyx*. The petals in *P. nitidus* are just opening, all others with petals fully expanded, 4 \times .

there are three vascular traces while in *P. linearis* and *P. crenatus* there are only two. These differences were noted in the examination of about 15 flowers of the five species with only one flower of *P. parryi* being anomolous in having four traces in the style.

Plants of the five species of *Petalonyx* are perennial but the growth form characteristic of each species ranges from woody only at the very base, as in *P. thurberi*, to a well developed but small shrub, as in

P. parryi. The leaves are simple but have a number of consistent differences of shape and margin, which distinguish the species.

Like most members of the Loasaceae, the plants of *Petalonyx* are covered with a harsh pubescence. *Petalonyx* has a type of trichome that also is found in all plants of the family, but unlike many genera, *Petalonyx* only has this "basic" type (fig. 6a, b). These trichomes are found in somewhat modified forms on different parts of the same individual and all of the taxa can be recognized by at least slight differences in the pubescence. *Petalonyx linearis* is most distinct in its pubescence in having short, truncate trichomes on the stems which contrast sharply with the long slender trichomes of the bracts and ovary. The pubescence of *P. parryi* and *P. nitidus* is quite similar but the stem pubescence in *P. parryi* is straight while in *P. nitidus* it is reflexed. The two subspecies of *P. thurberi* are distinguished primarily by a difference in pubescence with ssp. *gilmanii* having a finer, longer, and more dense pubescence than ssp. *thurberi*.

Meiosis has been observed in plants from six populations representing four of the five species of *Petalonyx*, including both ssp. of *P. thurberi*, with only *P. crenatus* remaining unknown chromosomally. All of the plants examined showed 23 pairs of chromosomes. Metaphase bivalents are approximately 3 micra long although in every cell examined there were slight but obvious differences in the size of the bivalents so that a continuous series from smaller to larger bivalents could be noted. Chromosome observations of *Petalonyx*, were made on the following collections: *P. linearis*, $n = 23$, N of San Felipe, Baja California, Mexico, *Raven 14791*; *P. nitidus*, $n = 23$, Panamint Springs, Inyo Co., California, *Thompson 3273*; *P. parryi*, $n = 23$, near Glendale, Clark Co., Nevada, *Thompson 3274*; *P. thurberi* ssp. *thurberi*, $n = 23$, 10 miles W of Kingman, Mohave Co., Arizona, *Thompson 3294*; 9 miles W of Randsberg, Kern Co., California, *Kyhos*, May 12, 1962; *P. thurberi* ssp. *gilmanii*, $n = 23$, Ryan Wash, Death Valley National Monument, California, *Davis 170*.

Information about the breeding system in *Petalonyx* is limited to that suggested by flower structure and seed set in natural populations. In *P. linearis* the stigma is located among the anthers at the time pollen is shed (fig. 1) and self-pollination in each flower seems inescapable. In the other four species the anthers are positioned well away from the stigma when the pollen is shed (fig. 1) and some vector must be necessary for pollination. In the herbarium specimens of *P. linearis* over 90 percent of the ovaries contain a seed while in the other four species seed set frequently is about 50 percent. This information, together with the floral morphology, suggests that *P. linearis* is highly self-pollinated, self-compatible, and hence an inbreeding species while the other four species are more highly outbreeding. Timberlake (1962, pp. 14, 36-38) suggests that the bees *Perdita exilis* Timberlake and *P. crandalli* Timberlake probably are oligolectic on *Petalonyx thurberi*

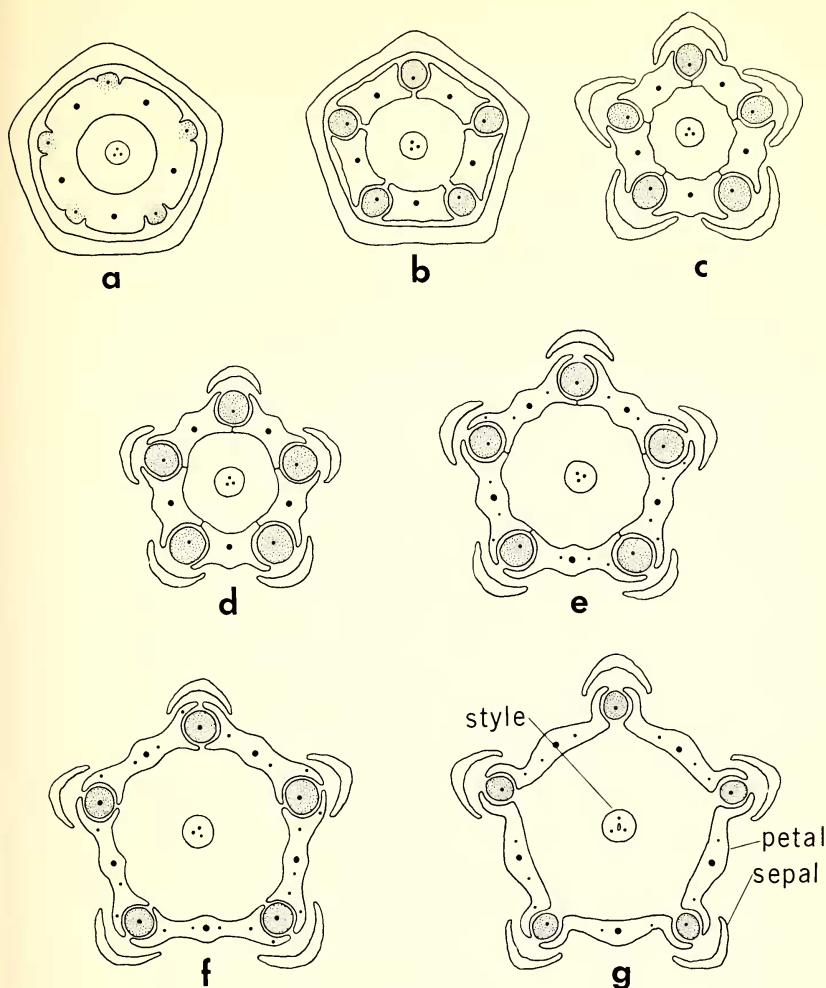


FIG. 2. Transverse sections through a flower of *Petalonyx thurberi* before anthesis (filaments stippled): a, section through the calyx tube and upper portion of the ovary; b, section through an area just above (a); c, section through the calyx lobes, petal claws, and style; d, section through an area above (c); e, section through an area above (d); f, section through an area above (e); g, section through an area above (f) showing the calyx lobes, petal limbs, filaments, and style.

and they may be important pollinators. The flowers of *P. thurberi*, *P. nitidus*, and *P. parryi* are lightly fragrant and attract a variety of insects, many of which could effect pollination.

Although all five species of *Petalonyx* are restricted to the arid regions of the southwestern United States and northern Mexico we have been unable to find two species growing in mixed or adjacent populations. This is because of the very limited ranges of two of the

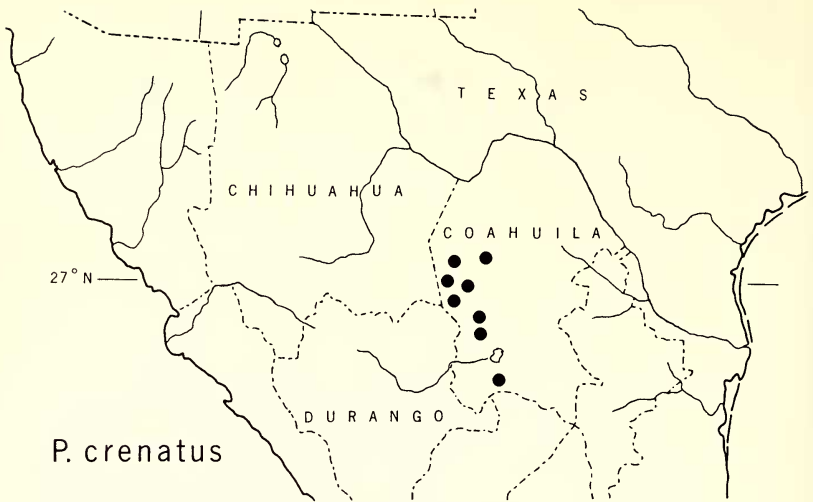


FIG. 3. Distribution of *Petalonyx crenatus*.

species, their different ecological requirements, and the small size of local populations. *Petalonyx crenatus*, morphologically very distinct with its slightly irregular flowers, narrow petals, and distinctive crenate leaves also is geographically isolated, growing only in western Coahuila, Mexico, where it is disjunct by 500 miles from the other species of the genus (fig. 3). *Petalonyx linearis*, also morphologically very distinct, occurs in sandy areas of the lower Colorado Valley and Vizcaíño regions of the Sonoran Desert (fig. 4) usually below 2500 feet elevation. The autogamous breeding habit and restriction to the geologically new desert habitats suggest a derivative status for *P. linearis*. *Petalonyx thurberi* also ranges into the Sonoran Desert and seems so similar to *P. linearis* in habitat preference that we are forced to ascribe our inability to find them growing together merely to chance. *Petalonyx thurberi*, *P. nitidus*, and *P. parryi* are not only morphologically similar to each other but they occur in the same general area (fig. 5). *Petalonyx thurberi* occurs in sandy areas and washes of the Mojave Desert and extends into the upper regions of the Sonoran Desert. It usually occurs at elevations between 1000 and 3000 feet although stations above and below these limits are not exceptional. *Petalonyx thurberi* ssp. *gilmanii* is restricted to the Death Valley region. *Petalonyx nitidus* occurs on more rocky soils in the Mojave Desert, usually above 3000 feet elevation and extending as high as 7000 feet. Where *P. thurberi* and *P. nitidus* occur in the same area we have found *P. nitidus* at higher elevations than *P. thurberi*. *Petalonyx parryi* is restricted to a local area near the Virgin and Colorado rivers in southern Nevada and adjacent Utah and Arizona (fig. 5). It is found at elevations below 3000 feet and is probably restricted to white to grey clay soils.

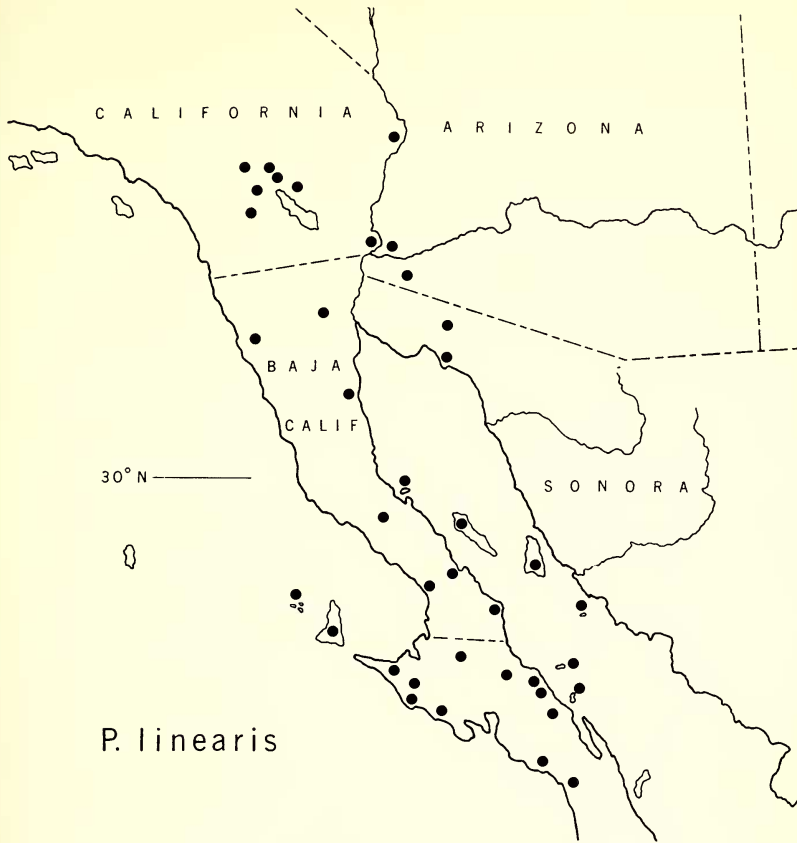


FIG. 4. Distribution of *Petalonyx linearis*.

The species of *Petalonyx* obviously are similar in many respects and the differences between them can be understood as variations on a basic theme. The question of which other group of populations in the Loasaceae is most similar to *Petalonyx* is not so readily answered. Similarity to *Cevallia*, *Gronovia*, and *Fuertesia* is suggested by the grouping of these genera with *Petalonyx* to form subfam. Gronovioideae on the basis of the single, pendulous ovule and the reduced number of stamens common to all four genera.

CEVALLIA

The single species of this genus, *C. sinuata* Lag., occurs in northern and eastern Mexico and the southwestern United States. The plants are low herbaceous perennials with only the basal stems becoming woody. The leaves are sinuate-pinnatifid and, like all members of Loasaceae, the plants are covered with a harsh pubescence. There are three different types of trichomes, all one-celled, which may occur side by side on a single organ. Some of the trichomes are like the basic type found

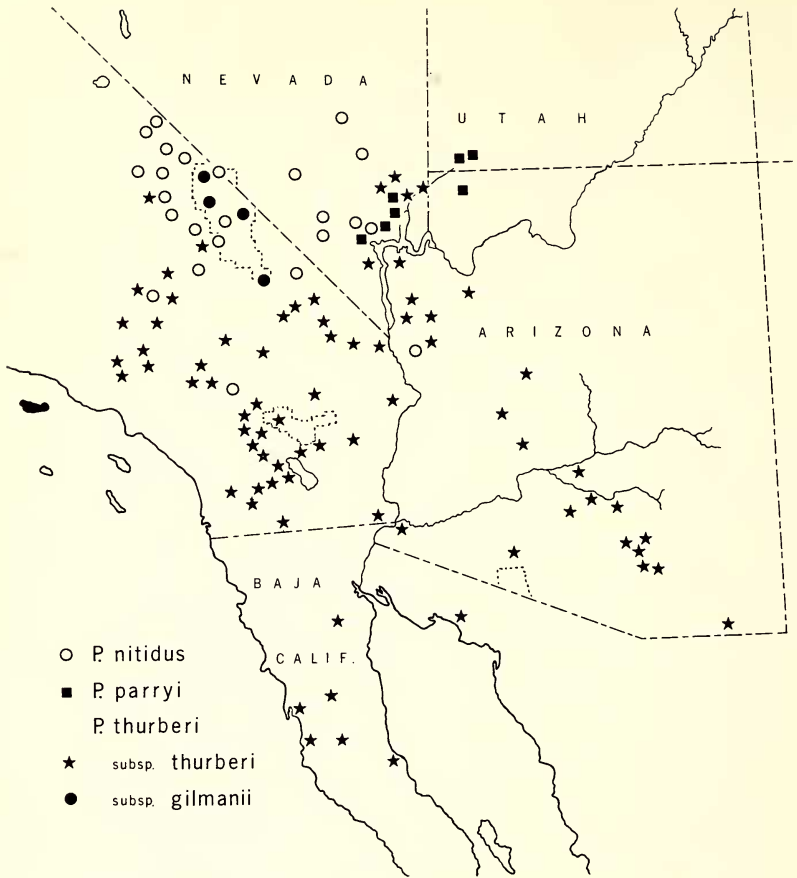


FIG. 5. Distribution of *Petalonyx nitidus*, *P. parryi*, and *P. thurberi*.

in *Petalonyx* and throughout Loasaceae (fig. 6a, b). A second trichome type is dendritic, 0.1 mm long, and forms a dense tomentum over much of the plant (fig. 6f). A third trichome type is up to 3 mm long, straight, without barbs but with a very acute apex (fig. 6e). The base of these trichomes is buttressed by a ring of numerous columnar epidermal cells. These trichomes probably are the ones that so readily penetrate human skin and account for the painful, stinging sensation when the plant is touched. The first two types of trichomes lack the basal, columnar cells that surround the base of the long trichome.

The flowers are clustered in tight heads at the ends of peduncles that are borne opposite the leaves. The ovary is inferior and produces one, pendulous seed that lacks endosperm. The cotyledons are ovate and smooth on the inner surface. The fruit is indehiscent with the sepals and petals persistent. There is no matrix tissue that develops about the

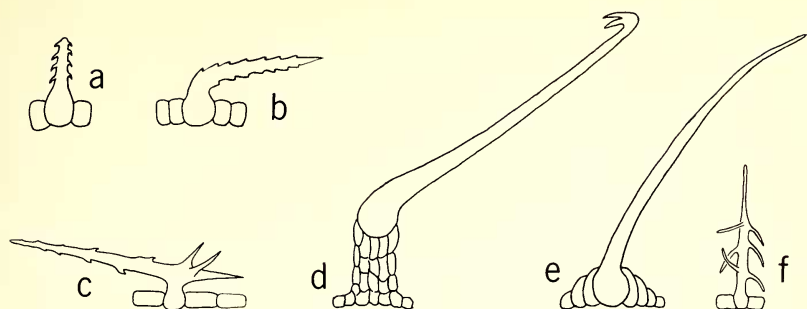


FIG. 6. Diagrams of longitudinal sections of trichomes in subfam. Gronovioideae: a, b, *Petalonyx*, 50 \times ; c, *Fuertesia*, 20 \times ; d, *Gronovia*, 20 \times ; e, *Cevallia*, 20 \times ; f, *Cevallia*, 15 \times .

ovule as in *Gronovia*. Atop the ovary is a short hypanthium from the outer edge of which arise ten similar segments, but there is no disc within the hypanthium. The five segments opposite the stamens usually are considered calyx-lobes while the other five are considered petals. Both series are erect, linear, very pubescent, and plumose by virtue of the long trichomes along the margins. When the flower opens and pollen is shed the petals are held inward about the stamens while the sepals are turned slightly outward. Both petals and sepals are yellow on the inner surface but the petals are somewhat brighter in color and are slightly less plumose. The five stamens arise from the top of the hypanthium with short, thick filaments and the anther is borne on the adaxial surface of the filament with the basal portion of the anther free. The connective extends well beyond the anther as a hollow, thin-walled, somewhat inflated appendage. The style is short and topped by a conical stigma that is positioned opposite the base of the anthers. Meiotic chromosomes have been observed in two plants from two different populations and each had 13 pairs of chromosomes. The chromosomes are all the same size and the metaphase bivalents are nearly five micra long. Chromosome observations of *Cevallia* were made on the following collections: *C. sinuata*, $n = 13$, 14 miles S of Mammoth, Pinal Co., Arizona, *Thompson 3221*; 33 miles N of Van Horn, Culbertson Co., Texas, *Thompson 3286*. In the Van Horn population the flowers were noted to have a faint fragrance and were visited by a great variety of insects, particularly bees and butterflies. Flower structure makes self-pollination inevitable but outcrossing might still obtain if the plants are self-incompatible.

GRONOVIA

The two species of this genus, *G. scandens* L. and *G. grandiflora* Urban & Gilg, are readily distinguished by differences in the size and proportions of the flowers but otherwise are so similar that for our purpose of characterizing the genus we need not distinguish between

them. *Gronovia* occurs throughout much of Tropical America from Venezuela and Ecuador to northern Mexico. The plants are herbaceous perennial vines with long petioled, simple leaves. The blades are broadly ovate with cordate bases and coarsely toothed, often 3–5 lobed margins. In addition to having the typical trichomes found throughout Loasaceae, (fig. 6a, b) the plants have a very characteristic trichome type that is about 3 mm long and is unarmed except that the apex is formed into a double hook (fig. 6d). These hairs are supported by a mass of columnar cells that surround the basal portion of the trichome cell and raise the base of this cell well above the level of the plane of the epidermis. This type of trichome occurs only on the stems and the adjoining portion of the petioles. The inflorescence is open and borne on peduncles that are opposite the leaves. The ovary is inferior, is topped by a disc with a crenate margin, and has one pendulous ovule. The single ovule is surrounded by a matrix of spongy tissue which is compacted as the seed enlarges and fills the ovary cavity after the seed is formed. The fruit develops five prominent, longitudinal ridges and is indehiscent. The seed lacks endosperm and the seed coat is membranous and unornamented. The cotyledons are ovate and their inner surfaces are strongly rugose. The ovary is topped by a short hypanthium from the rim of which extend five calyx-lobes. The petals are free, narrow, and rather inconspicuous. The stamens have slender filaments and a terminal, 4-celled anther. The style is slender and has a small, capitate stigma that is situated among the anthers. Meiotic chromosomes of one plant of *Gronovia scandens* have been examined. The 37 pairs of chromosomes were of equal size and somewhat smaller than those of *Cevallia* but larger than the chromosomes of *Petalonyx*. Chromosome observations were made from the following collection: *G. scandens*, $n = 37$, cultivated strain grown from seed obtained from the Botanical Garden, Copenhagen, culture number at Los Angeles, *Thompson 3234*. A mitotic chromosome count of $2n = 76$ was reported by Hamel (1938) for *G. scandens* growing in the Jardin des Plantes at Paris. We have readily cultured *G. scandens* in our greenhouse. The position of the anthers and stigma insure self-pollination and the formation of many viable seeds on the plants cultured in our greenhouse indicates that the plants are self-compatible.

FUERTESIA

This genus contains a single species, *F. domingensis* Urban, which is restricted to the island of Hispaniola in the West Indies. It differs from *Gronovia* in having lobed petals, an entire margined disc on the apex of the ovary, and a simple stigma, but in general appearance it is like *Gronovia*. The pubescence of *Fuertesia* consists of two different types of trichomes in addition to the basic type found in other genera of Loasaceae. The first type is like the double-hooked trichome found on the stem and basal portions of the petioles of *Gronovia* (fig. 6d) but

is shorter with a few barbs along its length. The second type of trichome is unique to *Fuertesia* and has been found only on the leaves (fig. 6c).

SUBFAMILY GRONOVIOIDEAE

Although our considerations of *Cevallia*, *Gronovia*, and *Fuertesia* were only peripheral to our monograph of *Petalonyx*, we feel some authority to comment on the affinities of these genera within the Loasaceae.

Gronovia and *Fuertesia* obviously are more similar to each other than to any other genera. They have similar forms, similar floral morphology, and share the unique bifid trichome which occurs nowhere else in the family. Although these two genera may be considered closely related, no such comparable relationship is indicated among the other genera. *Petalonyx*, *Cevallia*, and *Gronovia* were grouped by Urban and Gilg. in subfam. Gronovioideae by giving great weight to two characters: stamens 5 in number and ovary with a single seed. Emphasis of these two characters gives a distorted representation of the affinities among these genera. For example, while *Petalonyx* and *Cevallia* are similar in having 5 stamens, and thus are unlike all species of subfam. Mentzelioideae and subfam. Loasoideae, a different view is reached when the individual stamens are compared. In stamen morphology *Petalonyx* and *Cevallia* are more different from each other than either of these two genera are from any other genera in the family. Similar evaluations may be made about the number of seeds per capsule. Several species (e.g., *Mentzelia oligosperma*, *Fissenia* sp.) have the seeds reduced to 1-3 per capsule. Reduction in seed number occurs in conjunction with indehiscent capsules and small flowers in many otherwise distinct groups in Loasaceae. Furthermore, the information from chromosome numbers does not indicate any relationships among any of the genera currently grouped in subfam. Gronovioideae.

We consider *Petalonyx*, *Cevallia*, and the *Gronovia-Fuertesia* alliance, which now comprise subfam. Gronovioideae, to be three divergent groups whose affinities lie with other genera in the family and not with each other. However, until a more thorough study is made of all of the genera in this family none of the details of these similarities can be recorded in a formal taxonomic form and we must be content merely to have pointed out the very artificial basis of subfam. Gronovioideae.

TAXONOMY OF PETALONYX

PETALONYX A. Gray, Mem. Am. Acad. 5:319. 1855. Shrubs or subshrubs; leaves alternate, petioled or sessile, entire, toothed or crenate; inflorescence a naked or bracted raceme, or spicate raceme; each flower involucrate with three green bractlets at the summit of the pedicel, two of which are smaller and lateral; sepals joined to form a tube adnate to the ovary, cleft almost to the base, the lobes linear to lance-linear, inner surface glabrous, outer hispid, persistent or irregularly deciduous; petals cream to white, clawed, inner surface glabrous, outer hispid;

claws free or connivent to form a tube; limbs usually reflexed; stamens free, originating between, and apparently in the same whorl as the petals, outside the petals at anthesis and in bud curving inside and covered by the overlapping petals; anthers 4-celled; pollen elliptic, tricolpate, unornamented; style filamentous; stigma simple; mature fruit a uniloculate utricle, cylindrical; constricted near the apex, then flaring above, 3-5 nerved, with brittle, usually ribbed walls; ovule 1, without endosperm, pendulous; seed pointed at the hilum, unornamented or with fine striations on the testa; embryo with thick, plano-convex cotyledons and a short, acute, radicle.

Type Species: *Petalonyx thurberi* A. Gray.

KEY TO THE SPECIES

Petal distinct.

Anther bearing stamens 2, about twice as long as the petals, sterile filaments 3, about as long as the petals; leaf margins revolutely crenate; bractlets oblong, truncate at the base; petal limb less than twice as wide as the claw; Coahuila, Mexico. *P. crenatus*

Anther bearing stamens 5, equaling the petals in length; leaf margins entire or remotely dentate; bractlets ovate, the base cordate; petal limbs at least twice as wide as the claw: deserts of California, western Arizona, Baja California, Sonora, and the Islands of the Gulf of California
2. *P. linearis*

Petals connivent, the claws forming a tube.

Leaves sessile, reduced upward along the stems; petals shorter than 5 mm; widely distributed in the desert areas of southern California, Baja California and Arizona. 3. *P. thurberi*

Leaves petiolate, similar in size along the stems; petals longer than 5 mm.

Sub-shrubs, predominately herbaceous, current seasons growth longer than 10 cm; leaf margins coarsely few-toothed; inflorescence a bracted raceme; petals shorter than 11 mm; Inyo and San Bernardino of California to southern Nevada and northern Arizona above 3000 feet elevation. 4. *P. nitidus*

Shrubs, predominately woody, current seasons growth less than 10 cm long; leaf margins entire to crenate; inflorescence a naked, terminal raceme; petals longer than 11 mm; Coconino and Mohave counties of Arizona to southern Utah and Nevada, usually on white to grey clay soils and below 3000 feet elevation. . . . 5. *P. parryi*

1. *PETALONYX CRENATUS* A. Gray ex Watson, Proc. Am. Acad. 17:358. 1882. Suffruticose, with short, erect, brittle, herbaceous branchlets, up to 10 dm high; stems of the current season 10-20 cm long, to 6 mm wide, surface smooth, grey-green or yellow-green, densely hispid with long, pointed, antrorsely barbed, retrorsely appressed hair; older stems straw-colored to dark grey; leaves sessile, similar in size along the stems, 0.6-1 cm long, 0.2-0.4 cm wide, oblong-lanceolate, obtuse, cordate, revolutely crenate, green, hispid with fine, long, antrorsely barbed hairs on both surfaces, and short, truncate retrorsely barbed hair along the margins; inflorescence a terminal, naked raceme, 20-40 flowered, to 5 cm long, elongated in fruit, the lower fruit fallen; pedicels

1.0–2.5 mm long; large bractlet 3–5 mm long, 1.5–2.5 mm wide, triangular-ovate to oblong with a prominent midrib before maturity, acute, truncate to sub-cordate, crenate basally, hispid with long, pointed, antrorsely barbed hair; lateral bractlets 2–3 mm long, 1.5–2 mm wide, ovate to triangular-ovate, pinnately cleft, hispid; sepal lobes 1.5–2.5 mm long, 0.5–0.9 mm wide, recurved, persistent; petals white, linear to narrowly spatulate, acute, claw not sharply delimited from the limb, 4–7 mm long, 1–1.5 mm wide, not connivent; claw 0.7–0.9 mm wide, with short, epidermal papillae; two fertile stamens, well exerted, 10–11 mm long, three sterile stamens 5–9 mm long; filaments with basal epidermal papillae; anthers 0.5–0.6 mm wide; pollen 24.7–28.2 micra in diameter; style 5–10 mm long, shorter than fertile stamens; mature fruit 1.5–2.5 mm long, 1.1–1.5 mm wide at the base, 0.8–1 mm wide at the apex, hispid with pointed or truncate, retrorsely barbed hair to 0.4 mm long; seed 1.8–2 mm long, 0.8–1 mm wide. Chromosome number unknown.

Type. San Lorenzo de Laguna, 75 miles SW of Parras, Coahuila, Mexico, *Palmer 833*, in May of 1880 (GH, isotype US).

Distribution (fig. 3). Sandy plains, gypsum mesas, and dry trough-like valleys, Coahuila, Mexico.

Specimens examined. MEXICO. COAHUILA: About 30 miles S of Sierra Mojada, *Wynd 769*; Sierra del Rey, *Purpus 4466*; W base of Picacho del Fuste, *Johnston 8353*; 16 miles S of Laguna del Rey, *Johnston 7808*; near Mohovano, *Shreve 8831*; between La Vibora and Matrimonia Viejo, *Johnston 9348*; Rancho Parritas, E margin of the Valle de Acatita, *Stewart 2762*; Las Delicias, *Stewart 2959*; W of El Oro, *White 2006*; S end of Cañada Oscuro near Tanque La Luz, *Johnston 8487*.

2. *PETALONYX LINEARIS* Greene, Bull. Calif. Acad. 1:188. 1885. Suffrutescent, almost globose with numerous erect branches, 1.5–10 dm high; current seasons growth 10–38 cm long, to 6 mm wide, grooved, grey-green to dull green, scabrous with short, tapered, truncate, retrorsely barbed hair, perpendicular to the stem; older stems white to grey; leaves sessile to very short petioled, similar in size along the stems, 1–4.2 cm long, 0.3–1.5 cm wide, linear to oblanceolate, acute or occasionally obtuse, narrowed basally becoming cuneate to obtuse, entire or rarely remotely dentate, green and somewhat shiny, muricate-hispid with long, pointed, antrorsely barbed hair on the abaxial surface and truncate, retrorsely barbed hair on the adaxial surface, and mixed truncate and pointed hair along the margins; inflorescence a short, capitate, terminal spike, 30–60 flowered, 4–10 cm long, elongated in fruit to 21 cm, the lower fruit fallen; pedicels 1–2 mm long; large bractlet 5–8 mm long, 5–6 mm wide, ovate to round-ovate, acute to obtuse or rarely retuse, cordate to deeply cordate, entire, sinuate or minutely crenulate at the base, hispid on both surfaces and the margins

with long, fine, pointed, antrorsely barbed hair; lateral bractlets 3–3.5 mm long, 2–2.2 mm wide, ovate, acute to obtuse, sub-cordate, lobed, hispid; sepal lobes 1–2 mm long, 0.7–0.8 mm wide, erect, irregularly deciduous; petals white, 2–5.5 mm long; claw 1.4–3.1 mm long, linear, with no epidermal papillae, few hairs, and not connivent; limb 1.7–2.4 mm long, 1.3–1.4 mm wide, ovate, acute, hispid; stamens barely exerted, 3–7 mm long; filaments without epidermal papillae; anthers 0.3–0.5 mm wide; pollen 24.2–28.2 micra in diameter; style 2.8–6 mm long, nearly equal in length to the stamens, without epidermal papillae; mature fruit 5 nerved, usually 3 ribbed, 2–4 mm long, 1.2–1.6 mm wide at the base and 0.5–0.6 mm wide at the apex, pubescent with dense, long, pointed, retrorsely barbed, antrorsely appressed, easily deciduous hair, to 0.7 mm long; seed 2.3–2.5 mm long, 0.9–1 mm wide. Chromosome number, $n = 23$.

Type. Cedros Island, common in the canyons of the middle of the island, on the E side, Baja California, Mexico, *Greene*, May 1, 1885 (CAS).

Distribution (fig. 4). Occasional in rocky places in canyons but common in sandy soil below 3,000 ft.; Lower Sonoran Zone, Creosote Bush Scrub, California to southwestern Arizona, southward to Baja California, Sonora and the islands of the Gulf of California.

Specimens examined. *Petalonyx linearis* is well represented in U.S. herbaria and over 100 collections have been annotated.

3. *PETALONYX THURBERI* A. Gray, Mem. Am. Acad. 5:319. 1855. Suffrutescent, often broader than tall, to 10 dm high; stems of the current season 12–45 cm long, to 6 mm wide, striate or smooth, grey-green, hispid; older stems white or yellowish; leaves sessile, reducing in size along the branches, 0.4–4.5 cm long, 0.2–1.4 cm wide, variable in shape, deltoid-ovate to lanceolate, acute to acuminate, cuneate to cordate-clasping, entire to few toothed (teeth 0.3–1.8 mm long and 0–4 on each margin), grey-green, dull to somewhat shiny, hispid to densely hispid with long pointed antrorsely barbed hair; inflorescence a short, dense, naked, terminal, spicate raceme, 10–40 flowered, 1–4 cm long, slightly elongated in fruit; pedicels 0.2–0.7 mm long; large bractlet 3.2–7.5 mm long, 2.1–5.9 mm wide, deltoid-ovate to triangular-ovate, acute to somewhat acuminate, obtuse to sub-cordate, entire or crenate at the base (0–8 teeth per margin), hispid with dense, antrorsely barbed, pointed hair; lateral bractlets 2–3 mm long, 0.8–1.4 mm wide, lanceolate to ovate, unequally crenate to lobed, hispid; sepal lobes 1–2.2 mm long, 0.3–0.5 mm wide, erect, irregularly deciduous; petals cream colored, 2.6–6.5 mm long; claw linear, 1.4–4.1 mm long, 0.3–0.5 mm wide, hispid, without epidermal papillae, the upper one-fifth irregularly connivent; limb 1.2–2.5 mm long, 0.8–1.5 mm wide, ovate, acute, hispid; stamens well exerted, 5–10 mm long, coiled in bud; filaments without epidermal papillae; anthers 0.3–0.5 mm wide; pollen 23.5–29.4 micra in diameter;

style 3.7–11 mm long; mature fruit 1.6–3.1 mm long, 0.7–1.6 mm wide at the base, and 0.7–0.9 mm wide at the apex, obscurely five-ribbed or smooth, hispid to densely hispid with pointed, antrorsely barbed hair to 0.17 mm long; seed 1.6–2.5 mm long, 0.7–1.3 mm wide. Chromosome number, $n = 23$.

Type. Valley of the Rio Gila, Arizona, *Thurber*, June, 1850 (GH).

Distribution (fig. 5). Frequent in dry sandy places, sandy plains, desert washes, dry stream beds, or gravelly places below 4,000 ft., from Inyo Co., California, to Nevada, Arizona, Sonora, and Lower California.

Although this species is the most widely distributed of the five, it is morphologically uniform and only two distinct population groups have been noted and only one of these is given subspecific recognition in this study. Subspecies *gilmanii* is restricted to Inyo Co., California and will be discussed below. The other morphologically distinct populations are distributed in Imperial Co., California, and Baja California. The leaves on plants from these areas are on the average slightly smaller than *P. thurberi* ssp. *thurberi* and are closely appressed to the stems. The remainder of the vegetative and floral characters are within the range of plants of *P. thurberi* ssp. *thurberi* from other areas and for this reason we have not accorded subspecific recognition to these populations.

KEY TO SUBSPECIES

- Leaf and stem pubescence harsh, retrorsely appressed on the stems, stamens longer than 6 mm, widely distributed and common throughout the deserts of California, Arizona, Nevada, Baja California, and Sonora 3a. ssp. *thurberi*
 Leaf and stem pubescence very soft, perpendicular to the stems, stamens less than 6 mm long, restricted to Inyo Co., California 3b. ssp. *gilmanii*

3a. PETALONYX THURBERI ssp. THURBERI. Plants 3–8 dm high; current seasons growth 22–45 cm long; stems grooved, hispid, with retrorsely appressed hair; leaves 0.6–4.5 cm long, 0.2–1.4 cm wide, lanceolate to lance-ovate, acute to acuminate, cuneate to truncate, somewhat shiny, hispid on both surfaces; petals pale cream to white, 2.6–6.5 mm long; stamens 6.0–10.0 mm long; style 5.0–11.0 mm long. Chromosome number, $n = 23$.

Distribution (fig. 5). Frequent in dry sandy places, Lower Sonoran Zone, Creosote Bush Scrub, *Covillea* and *Artemisia* belts, Mojave and Colorado deserts, from Inyo Co., California, to Nevada, Arizona, Sonora, and Baja California.

Specimens examined. *Petalonyx thurberi* ssp. *thurberi* frequently is collected and is well represented in U.S. herbaria. Over 150 collections have been annotated.

3b. PETALONYX THURBERI ssp. *gilmanii* (Munz) Davis & Thompson, n. comb. *Petalonyx gilmanii* Munz, Leaflet West. Bot. 2:69. 1938. Plants up to 10 dm high; current seasons growth 12–21 cm long; stems not grooved, densely hispid with long hair, perpendicular to the stems; leaves 0.4–2 cm long, 0.4–1.3 cm wide, deltoid-ovate, acute to abruptly

acuminate, truncate to cordate-clasping, dull, never shiny, densely hispid on both surfaces; petals pale cream, 2.9–4.1 mm long; stamens 5–7.5 mm long; style 3.7–6 mm long. Chromosome number, $n = 23$.

Type. Ryan Wash, Death Valley, at 1500 ft. elevation, Inyo Co., California, *M. French Gilman 1568*, May 20, 1937 (POM 228696; Iso-type frag. CAS).

Distribution (fig. 5). Rare in washes and canyons, restricted to Inyo, California.

Specimens examined. CALIFORNIA. Inyo Co.: along road to Ryan, Death Valley, *Davis 170*; Cottonwood Canyon, Panamint Mountains, *Coville & Gilman 308*; 20 miles N of Stovepipe Wells Hotel, *Coville & Gilman 156*; Furnace Creek Canyon, Funeral Mountains, *Coville & Funston 356*; 5 miles NW of Saratoga Springs, *Coville & Funston 249*; Furnace Creek, Death Valley, *Parrish 10047*; Ubehebe Crater, Death Valley, *Kerr* in 1940; Ubehebe Crater Wash, *Gilman 2681, 3374, and 3377*; Slopes of Ubehebe Crater, *Gilman 2101*; Trona highway, Panamint Valley, *Twisselman 5843*.

In general, ssp. *gilmanii* has smaller flowers, broader leaves, and longer finer pubescence than ssp. *thurberi*. In addition, the stem hair is erect in *gilmanii* instead of appressed as in *thurberi*, and the current seasons growth generally is shorter than in *thurberi*.

4. PETALONYX NITIDUS Watson, Am. Nat. 7:300. 1873. *Petalonyx thurberi* var. *nitidus* (Watson) M. E. Jones, Contr. West. Bot. 12:16. 1908. Suffructicose with many erect branches, 1.5–4.5 dm high; current seasons growth 13–37 cm long, to 8 mm wide, not grooved, grey-green to dull green, scabrous with short, pointed antrorsely barbed hair, mostly antrorsely appressed; older stems straw-colored to dark gray; leaves petiolate, similar in size along the branches, 1.5–4.5 cm long, 1–3 cm wide, ovate to broadly ovate, acute to shortly acuminate, obtuse to rarely truncate, serrate to coarsely few-toothed (teeth 0.7–3 mm long and 2–8 on each margin), dark green, vernicose, muricate-scabrous on both surfaces with short, pointed, antrorsely barbed hair and on the margins with short, truncate, antrorsely barbed hair; petiole 0.8–5 mm long; inflorescence a terminal bracted raceme, 10–30 flowered, 3–4.5 cm long, not particularly elongated in fruit; pedicels 1–2 mm long; large bractlet 4.8–13.2 mm long, 2.1–7.9 mm wide, lance-ovate, acuminate, truncate, crenate with 3–7 teeth on each margin, scabrous with short, pointed, antrorsely barbed, appressed hair on both surfaces, and short, stout, truncate, retrorsely barbed hair on the margins; lateral bractlet 1–5 mm long, 1–2.4 mm wide, elliptic to ovate, acute to shortly acuminate, crenate along the basal margins, hispid; sepal lobes 1.4–3 mm long, 0.5–0.8 mm wide, irregularly deciduous; petals cream colored, 5–11 mm long; claws linear, 3.9–7 mm long, 0.3–0.4 mm wide, hispid along the upper one third, the upper one fourth connivent, the lower portion without epidermal papillae; limbs 1.5–3 mm long, 1.7–1.9 mm

wide, ovate, acute; stamens well exerted, 7–14 mm long, filaments with scattered epidermal papillae at the base; anthers 0.5–0.7 mm wide; pollen 24–29 micra in diameter; styles 8–15 mm long, usually shorter than the stamens; mature fruit five nerved and five ribbed, 1.3–3.1 mm long, 1–1.5 mm wide at the base, 0.7–0.8 mm wide at the apex, hispid with short, slightly tapered, truncate, retrorsely barbed hairs to 0.08 mm long; seed 2–2.2 mm long, 1.2–1.3 mm wide. Chromosome number, $n = 23$.

Type. Southern Nevada, *Wheeler* in 1871 (GH).

Distribution (fig. 5). Common in rocky canyons, washes of open desert, and sandy road banks above 3500 ft. Mojave Desert; Creosote Bush Scrub; Joshua Tree Woodland; and Pinyon-Juniper Woodlands. Inyo and San Bernardino counties of California, to southern Nevada, southwestern Utah, and northwestern Arizona.

Specimens examined. *Petalonyx nitidus* is well represented in U.S. herbaria and we have annotated over 50 collections.

We have encountered one collection of *P. nitidus* that falls well outside of the normal distribution of this species. This collection by Marcus Jones from Yucca, Arizona, is labeled *Jones 4483*, May 15, 1884. Although Jones' itinerary indicates that he was collecting around Yucca on May 15, 1884, it is also recorded that *number 4483* was collected on Sept. 11, 1884 at El Paso, Texas. The uncertainty concerning the collection is unfortunate since some of the specimens appear to be vegetatively intermediate between *P. thurberi*, which Jones did collect from Yucca, Arizona (*Jones 3936*, May 20, 1884) and *P. nitidus*. The presence of *Jones 4483* probably accounts for the inclusion of *P. nitidus* in the *Flora of the Sonoran Desert* (Shreve and Wiggins, 1964).

5. PETALONYX PARRYI A. Gray, Proc. Am. Acad. 10:72. 1874. *Petalonyx nitidus* ssp. *parryi* (A. Gray) Urban & Gilg, Nova Acta Acad. Leop.-Carol. 76:20. 1900. Fruticose, 8–15 dm high; stems of the current season usually less than 13 cm long, to 10 mm wide, not grooved, pale green to straw-colored, scabrous with scattered, short pointed, retrorsely barbed hairs, perpendicular or antrorsely appressed; older stems white-grey to dark grey; leaves petiolate, similar in size along the stems, 1.5–4 cm long, 1.2–3 mm wide, oblong-ovate to broadly elliptic, acute to obtuse, obtuse, entire or crenate (teeth 0.3–1.2 mm long and 5–12 on each margin), grey-green to yellow-green, usually not shiny, muricate-scabrous with short, pointed, strongly appressed hairs on both surfaces and short, pointed, strongly curved hairs on the margins; petiole 0.5–2.3 mm long; inflorescence a naked, spikelike, raceme, congested apically, up to 65 flowered, 4–8 cm long, elongated somewhat in fruit, the lower fruit fallen; pedicels 1–2.5 mm long; large bractlets 6.3–14 mm long, 2.4–10.1 mm wide, lanceolate to lance-ovate, acuminate, obtuse to truncate, crenate to dentate basally with 3–13 teeth per margin, hispid to scabrous with short, pointed, antrorsely barbed, ap-

pressed hair on both surfaces and short, truncate, retrorsely barbed hair on the margins; lateral bractlets 2.5–2.7 mm long, 1.3–1.6 mm wide, ovate, acuminate, dentate-crenate basally, hispid; sepal lobes 2.5–4 mm long, 0.5–0.9 mm wide, erect, irregularly deciduous; petals cream colored, 10–15 mm long; claws linear, 6.3–9.8 mm long, 0.3–0.4 mm wide, the upper one-half connivent, no epidermal papillae basally; limb 2.9–5 mm long, 1.7–2.3 mm wide, ovate, acute to obtuse, hispid; stamens well exerted, 11–17 mm long, filaments without epidermal papillae; anthers 0.6–0.8 mm wide; pollen 24–28.1 micra in diameter; style 11–15 mm long, generally shorter than the stamens; mature fruit five nerved and five ribbed, 2–4 mm long, 1.5–1.6 mm wide at the base, 0.8–0.9 mm wide at the apex, hispid with short, conical, truncate or pointed hairs, antrorsely barbed, to 0.15 mm long; seed 2.5–2.6 mm long, 1–1.2 mm wide. Chromosome number, $n = 23$.

Type. St. George, southern Utah, *C. C. Parry 75*, 1874 (GH). According to Parry (1875, p. 144) the type collection was taken from a single plant "within a stone's throw of the great Mormon Temple."

Distribution (fig. 5). In dry washes and on low slopes, usually on white to grey clay soils and below 3000 ft.; from Coconino and Mohave counties, Arizona, to southern Utah and Nevada.

Specimens examined. *Petalonyx parryi* is well represented in U.S. herbaria and over 25 collections have been annotated.

Although very similar to *P. nitidus* in floral morphology, *P. parryi* is vegetatively distinct. For example, *P. parryi* is woodier, and the leaf margins are crenate rather than dentate as in *P. nitidus*. The morphological distinctions between the two are quite sharp, and these along with ecological differences support the maintenance of these two as separate species.

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LITERATURE CITED

- HAMEL, J. L. 1938. Étude de la mitose somatique et numération chromosomique chez quelques Loasacées. *Revue Cyt. Cytophys. Vég.* 3:153.
PARRY, C. C. 1875. Botanical observations in southern Utah. II. *Am. Nat.* 9:144–146.
SHREVE F., and I. L. WIGGINS. 1964. Vegetation and flora of the Sonoran Desert. Vol. 2. Stanford Univ. Press.
TIMBERLAKE, P. H. 1962. A revisional study of the bees of the genus *Perdita* F. Smith, with special reference to the fauna of the Pacific Coast. *Univ. Calif. Publ. Ent.* 28:1–124.
URBAN, I., and E. GILG. 1900. *Monographia Loasacearum*. *Nova Acta Ocad. Leop.-Carol.* 76:10–22.